

## TWO RARE FOSSIL CONES FROM THE UPPER TRIASSIC CHINLE FORMATION IN PETRIFIED FOREST NATIONAL PARK, ARIZONA, AND NEW MEXICO

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**ABSTRACT** --- Although the Upper Triassic Chinle Formation in the southwestern United States contains a large flora of about 100 species, they are mostly based on foliar and stem material and only eight are based on cones. In this paper, we present the results of our investigation of two additional species of cones collected from the Chinle Formation in Petrified Forest National Park, Arizona, and from equivalent strata in west-central New Mexico. One is a seed cone described as *Araucarites rudicula* sp. nov.; the other is a pollen cone of uncertain affinity which is described as *Creberanthus bealeii* gen. et sp. nov. The identification of a cone with probable araucarian features is significant because it indicates that the Araucariaceae apparently extended into the Carnian stage of the Late Triassic, and is the first evidence of araucarian conifers in the Chinle impression/compression flora. The morphology of the cone *C. bealeii* indicates affinities with the pteridosperms, and that it is probably related to the somewhat similar pollen cone *Pramelreuthia*, which was recently recognized in the Chinle Formation. This fossil is noteworthy because it demonstrates that pteridosperms were a more diverse and significant component of the Chinle flora than previously realized. The cone is also significant because it contains pollen comparable to the dispersed pollen grain *Alisporites opii* Daugherty, which was originally described from the Chinle Formation in Petrified Forest National Park.

**Keywords:** *Alisporites opii*, Arizona, Chinle Formation, cones, Upper Triassic, Araucariaceae.

### INTRODUCTION

PALEOBOTANICAL INVESTIGATIONS of the Chinle Formation, especially in the parts exposed in Petrified Forest National Park, Arizona, have revealed one of the richest and most thoroughly documented Triassic plant assemblages in the world. Representatives of nearly every major vascular plant group, along with many problematic taxa, have been described from the flora (Ash, 1989). Due to the magnitude of this flora, the dominant taxa and/or those of particular phylogenetic, paleoecological, and paleobiogeographical interest were given research priority in the past. Consequently, several potentially significant plant fossils were temporarily set aside pending the discovery of more informative specimens. After nearly four decades of intensive collecting and analysis of the Chinle flora by the junior author, a clearer picture has emerged as to which taxa will probably not be significantly augmented by more satisfactory material, but still merit description. Two such forms are presented here, because they may have important implications for our understanding of more common components of the Chinle flora.

Both of the new taxa are represented by cones. The first is a coniferous ovulate cone here assigned to a new species of *Araucarites* Presl, 1838. This material provides the first convincing evidence of probable araucarian

conifers from the Chinle impression/compression flora. In addition to providing additional evidence for Chinle conifer diversity, this find has potential implications for the interpretation and affinities of the famous *Araucarioxylon arizonicum* Knowlton (in Fontaine and Knowlton, 1890), tree trunks preserved in such abundance in Petrified Forest National Park and elsewhere in the southwestern United States (Ash and Creber, 2000). The second described taxon, which is here placed in a new genus and species, is represented by only two fragmentary specimens of a lax cone bearing lateral synangiate organs with *in situ* bisaccate pollen. Although fragmentary, this material is significant because it adds to a growing realization of greater pteridosperm diversity in the Chinle flora than previously recognized (Ash and Litwin, 1996). We also demonstrate that this cone is the probable source of the dispersed pollen species *Alisporites opii* Daugherty, which is the type species of an important Triassic pollen genus and one of the most common Chinle Formation palynomorphs (Daugherty, 1941).

### PREVIOUS INVESTIGATIONS

In contrast to foliar and stem remains, fossil cones are quite rare in the Upper Triassic Chinle Formation and equivalent units in the western United States. Accord-

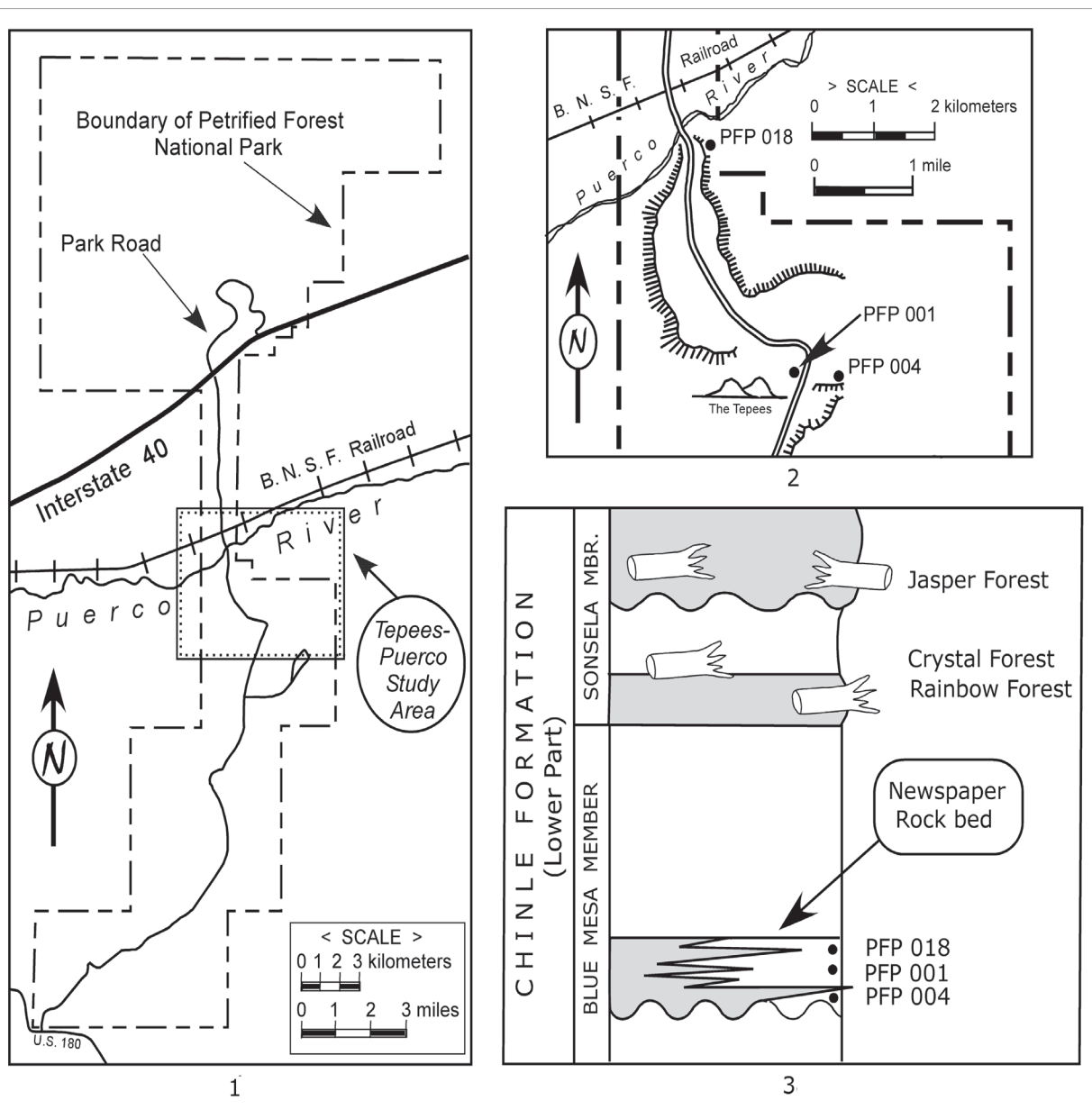


Figure 1. Maps of Petrified Forest National Park, Arizona and the Tepees-Puerco study area together with a simplified stratigraphic section of the lower part of the Chinle Formation in the area. The positions of the three localities that contained the fossils described here are shown by the large solid dots on the maps and their stratigraphic horizon is indicated on the chart by the same symbol. Information about the localities is contained in the text. Maps adapted from the topographic maps of the park (U.S. Geological Survey) and the chart is adapted from Ash (1987).

ing to a recent compilation by the junior author, of the approximate 100 well-defined species (assigned to 72 genera) of gymnosperms and non-gymnosperms now recognized in these units only eight, excluding the two described here, are represented by more or less complete cones. The previously described cones are one species each of *Equiclastrobus* Grauvogel-Stamm and Ash, 1999 and *Alostrobus* Ash, 1999 and two species each of *Masculostrobus* Seward, 1911 (Ash, 1972, 1999), *Pramelreuthia* Krasser, 1918 (Ash and Litwin, 1996) and *Williamsonia* Carruthers, 1870 (Ash, 1968).

## MATERIALS AND METHODS

All but one of the fossils described here were obtained from three localities in the central part of the park in the Tepees – Puerco River study area (Fig. 1). One specimen came from a locality in generally equivalent beds in the Fort Wingate area of west-central New Mexico (Ash, 1973).

The fossils collected in the park occurred in a thick bed of greenish mudstone that is laterally equivalent to the Newspaper Rock bed in the Blue Mesa Member of the

Chinle Formation (Fig. 1). The unit, called "leaf shales" by Stagner (1941), is widely exposed in the Puerco-Tepees area and, as he noted, contains plant fossils at several localities. It has also been termed the "wetland facies" of the Newspaper Rock bed fluvial deposits by Demko (1995) based on his hypothesis that it was deposited during repeated overbank floods on the floodplain of the stream that deposited the Newspaper Rock bed. The bed of mudstone is typically structureless and lacks bedding planes. Plant megafossils found in the deposit include large portions of leaves, small herbaceous stems, and occasional cones and cone parts, all of which are usually preserved as compressions. A few petrified stems are also known from the deposit. Although they are not abundant as plant fossils, the remains of aquatic organisms, such as crayfish, conchostracans, insects, and fish eggs have been found in the same deposit.

Demko (1995) contended that the plant megafossils found in the wetland facies in such abundance represent overbank vegetation (i.e., remains of plants that inhabited the floodplain). However, the plant megafossils typically are irregularly distributed and oriented in the deposit and few if any appear to be preserved in the position of growth. In fact, the general jumbled arrangement of the fossils suggests that most were washed onto the floodplain from elsewhere in a slurry of mud when the stream that deposited the Newspaper Rock bed overflowed its banks. The remains of aquatic organisms listed above that are found in the unit presumably represent organisms that were washed onto the floodplain or inhabited small ponds on the floodplain, although no lacustrine deposits have been recognized in the wetland facies.

The wetland facies is slightly different at locality PFP 018 of this paper than at other localities (e.g., locality PFP 001) because it contains a few thin (1-6 mm in thickness) and irregular clay partings that show abundant small fragments of plants and rare large portions of leaves and cones. The fossils in these partings appear to represent surface litter washed onto and deposited on the floodplain. Since these partings are irregular in distribution and thickness, they most probably represent random rather than seasonal events. Otherwise, the structureless green mudstone at this locality is similar to that found elsewhere and also contains a similar variety of irregularly distributed plant megafossils.

The description of the new *Araucarites* species is based upon only seven articulated cones, five isolated lateral appendages (bract/scales), and a possible isolated seed all collected from locality PFP 018 near the Puerco River. The cones and isolated bract/scales are preserved as stained impressions on thin clay partings in greenish mudstone with varying amounts of thick, coaly organic material, which tends to break up into sub-millimeter sized fragments when re-

moved from the matrix. So far, efforts at isolating cuticles from this material have been unsuccessful. The bract/scales have a tendency to split through the interior tissues revealing the internal vascular strands (Fig. 3.3); however, critical surface details are obscured in these specimens. Fortunately, two isolated bract/scales split along the adaxial surface-matrix interface and, therefore, show the ovule attachment scar. Limited dégagement was required to completely expose some of the cones and bract/scales. The thick carbonaceous residue of the bract/scales and the manner in which they cleave indicates that they most probably were thick, hard, and woody when living.

The new pollen cone described here is known from only two partial cones collected from two localities one of which is adjacent to the small hills called the Tepees in the central part of the park and is designated locality PFP 001. The second locality is about 250 meters east of locality PFP 001 across the main park road and is designated locality PFP 004. Daugherty (1941) first described plant fossils from both of these localities and was followed by several other workers (e.g., Gottesfeld, 1972; Litwin, 1985).

The new pollen cones are preserved as impression/compressions in greenish mudstone. Some parts of the impression are stained red. Dégagement was required to fully expose the lateral synangiate organs, because they occur at different levels within the matrix. The central axes have small amounts of dark organic matter attached. A few of these fragments were removed with needles and macerated in  $\text{HNO}_3$  and  $\text{NH}_4\text{OH}$ , but no cuticles were recovered. Some of the synangia are represented by compressed organic material. Using needles, this material was removed from one synangium per pollen organ and macerated in  $\text{HNO}_3$  and  $\text{NH}_4\text{OH}$ . A few pollen grains were teased out from the pollen masses with needles to allow for individual examination. The pollen masses and individual grains were mounted in glycerine jelly on glass slides for light microscopic examination.

## SYSTEMATIC PALEONTOLOGY

Family ARAUCARIACEAE Henkel and Hochstetter,  
1865

Genus ARAUCARITES Presl, 1838 (in Sternberg, 1838)

ARAUCARITES RUDICULA new species

Figures 2-4

*Diagnosis.*—Cone elongate (at least 6.35 cm long and 1.94 cm wide), lax; lateral appendages (bract/scales) spirally arranged on a narrow (~ 1.5 mm) central axis; individual lateral bract/scales with distinct basal stalk (average 1.6 mm long and 1.0 mm wide) and an expanded, wedge-

shaped distal portion (average 8.5 mm long and 8.0 mm wide at widest point near apex), thick and woody with numerous parallel vascular strands, adaxial surface of expanded region with shallow, proximal ovoid depression probably representing ovule attachment area, distally both surfaces with a convex, transverse furrow ~ 2.0 mm below apex, apical extension (area distal to furrow) relatively weakly lignified, rapidly contracting distally to a mucronate tip.

*Etymology.*—The specific epithet “*rudicula*” is the Latin term for wooden spoon, which refers to the typical appearance of the bract/scales.

*Types.*—Specimen PEFO 34141A, which includes an articulated cone (Fig. 2.1), is here designated the holotype. The counterpart is specimen PEFO 34141B (Figure 2.2). Paratypes consist of another nearly complete cone PEFO 34142 (Fig. 2.3); several partial articulated cones, including specimens USNM 528904 (Fig. 2.5), PEFO 34143 (Fig. 2.6), PEFO 34144 (Fig. 2.4); and isolated bract/scales, including specimen PEFO 34145 (Fig. 3.2).

*Other material examined.*—Unfigured cone and isolated lateral appendage material includes specimens PEFO 34146–34150. An isolated seed possibly attributable to *Araucarites rudicula* is specimen PEFO 34145 (Fig. 3.5).

*Occurrence.*—*Araucarites rudicula* n. sp. is presently known from one site (PFP 018) in the Blue Mesa Member of the Chinle Formation in Petrified Forest National Park, and one site in the Monitor Butte Member of the Chinle Formation in the Fort Wingate area (Fig. 2.5).

*Description.*—Only two complete or nearly complete cones and four partial articulated specimens of *A. rudicula* are known. The holotype is the best-preserved specimen and is represented by part (Fig. 2.1) and counterpart (Fig. 2.2). It is the only specimen with nearly complete lateral appendages in plan view. This specimen and the other nearly complete cone (Fig. 2.3) are the only specimens revealing much of the main axis. Therefore, it must be emphasized that most of our concept of *A. rudicula* is based on two specimens, and is likely to be expanded or modified if more material is recovered.

Both of the nearly complete cones are isolated with no indication of a peduncle preserved. They are both elongate and narrow. The holotype cone (Fig. 2.1, 2.2) was at least 5.64 cm long and 1.63 cm wide with a narrow axis ~1.5 mm wide. The second relatively complete cone (Fig. 2.3) was at least 6.35 cm long and 1.93 cm wide. The widest specimen is a only slightly wider partial cone (1.94 cm) (Fig. 2.4).

The lateral appendages, which probably represent fused bract/scale complexes like those of extant araucarians (and will be referred to as “bract/scales” throughout this paper), are helically arranged and lax on the cone axis (Fig. 2.5). On most specimens, the bract/scales are compressed

at various angles and are, therefore, difficult to interpret morphologically (e.g., Fig. 2.5, 2.6). Several of the bract/scales are covered with coaly residue indicating a thick and woody composition (Fig. 3.1).

The individual bract/scales consist of a proximal stalk-like region averaging 1.6 mm long and 1.0 mm wide (Fig. 2.5, 2.6, 4) and an expanded, wedge-shaped distal portion averaging 8.5 mm long and 8.0 mm wide at the widest point near the apex (Fig. 2.4, 2.5, 3.1, 3.2, 4). The best preserved example (Fig. 3.1) from the mid-region of the holotype cone was probably typical, and was at least 8.0 mm long with a narrow (1.7 mm wide) stalk-like base of uncertain length due to incomplete preservation, and an expanded, wedge-shaped distal portion 6.6 mm long and 7.0 mm wide at the widest point. Bract/scales from the upper parts of the cone, as well as several from partial cones (Fig. 2.5, 2.6) indicate that the stalks could be rather long and narrow (up to 2.5 mm long and 1.6 mm wide). Both surfaces of the expanded portion of the bract/scales possess a convex transverse furrow across the widest part (Fig. 2.4, 3.1, 3.2). The apical extension (i.e. the area distal to the transverse furrow) is up to 2.0 mm long and relatively weakly lignified. On many specimens this area is not preserved at all or is only weakly indicated (Fig. 3.2) giving the false impression that the bract/scale apex is rounded. However, better-preserved specimens indicate that the true appendage apex occurred distally to the furrow. The tip of the apical extension is not well preserved on any of the appendages observed so far, but was probably mucronate based on the broken tip bases sometimes visible (Fig. 3.1). A suggested reconstruction of a complete bract/scale in adaxial view is presented in Figure 4.

In some specimens, such as the holotype, the bract/scales split along the plant surface/matrix interface revealing the abaxial surface. In these specimens, the part has abundant coaly material present (Fig. 2.1, 3.1), whereas the counterpart is mostly represented by an impression (Fig. 2.2). In other specimens, the lateral appendages tend to split through the internal tissues revealing the numerous parallel vascular strands and/or fibers (Fig. 2.4, 3.3). The presence of such multiple vascular strands provides convincing evidence that these cones are of coniferous rather than lycopodlean affinity. Only two isolated appendages are preserved with the adaxial surface visible. On both specimens, a shallow, ovoid depression occurs near the base of the expanded portion of appendage. On the figured specimen (Fig. 3.4), the depression is 2.5 mm long and 1.7 mm wide; on the unfigured specimen it is 3.8 mm long and 1.9 mm wide. This depression is probably the attachment site of a single ovule.

An isolated ovoid seed-like structure 4.0 mm long and 2.25 mm wide is closely associated with an isolated



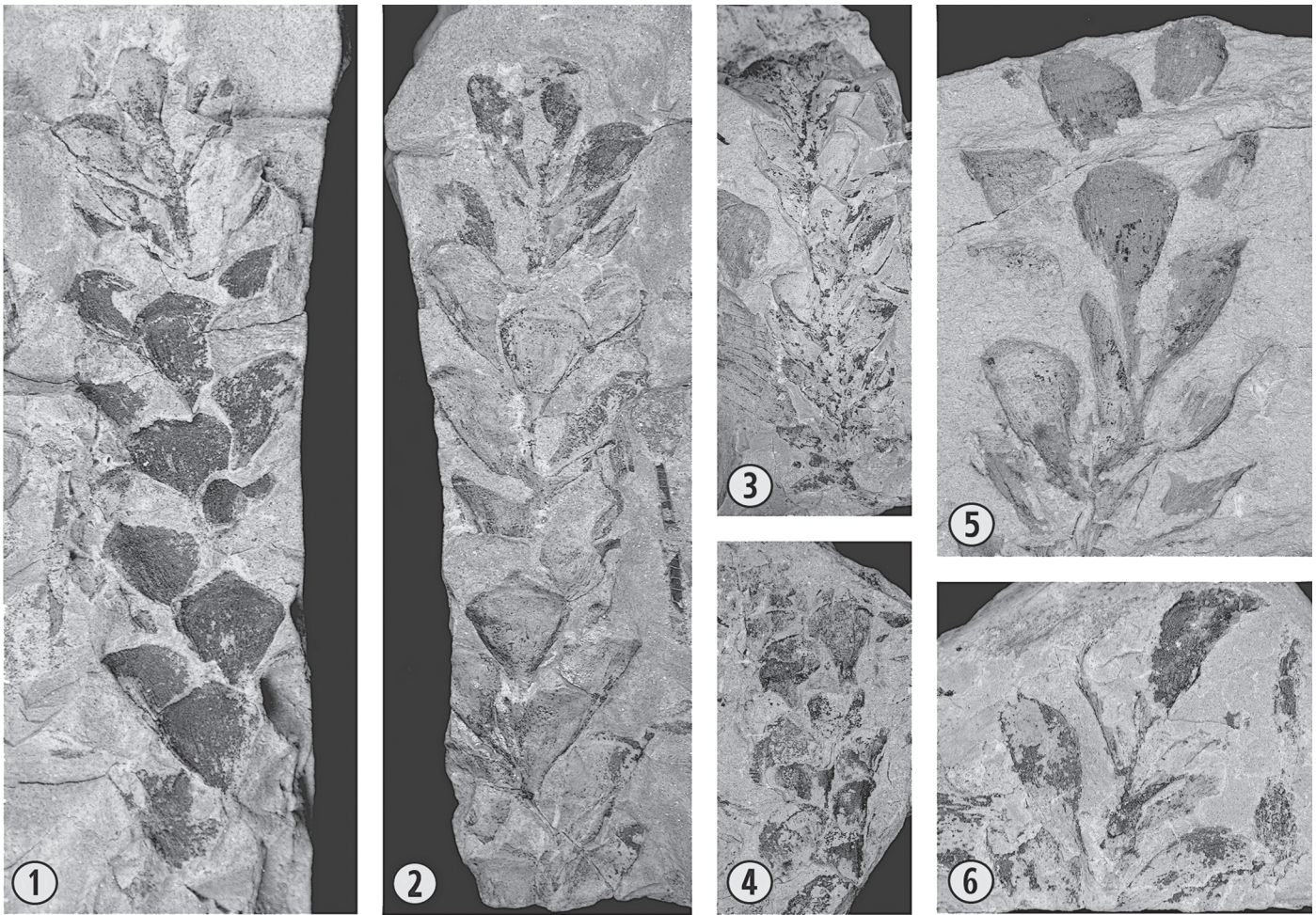


Figure 2. *Araucarites rudicula* sp. nov. 1. Articulated cone in longitudinal view with adhering organic material. The cone scale marked with an arrow is shown at a higher magnification in Fig. 3.1. Holotype.  $\times 2$ , PEFO 34141A; 2. Counterpart of holotype,  $\times 2$ , PEFO 34141B; 3. Articulated cone.  $\times 1$ , PEFO 34142; 4. Cone with bract/scales in plan view.  $\times 1$ , PEFO 34144; 5. Apical region of a specimen from Fort Wingate, NM showing elongate bract/scale bases.  $\times 2$ , USNM 528904; 6. Cone apex showing distorted shape of laterally compressed bract/scales.  $\times 2$ , PEFO 34143.

scale and partial cone (Fig. 3.5). At least one end is flattened (the opposite end is broken off). The seed surface bears many shallow, ovoid depressions about 1.0 mm in diameter. This structure is about the correct size and shape to qualify as the potential seed of *A. rudicula* based on the bract/scale depressions, but this cannot be proved based on one isolated specimen.

**Comparisons**—Due to the uncertain status of many fossils attributed to *Araucarites*, including unresolved issues regarding the genus name and type material (Buzek et al, 1968; Zijlstra and van Konijnenburg-van Cittert, 2000), comparisons are difficult. For example, reports of *Araucarites* appear sporadically throughout the Late Paleozoic and Early Mesozoic paleobotanical literature of Europe and Asia. Many of these references occur in obscure or difficult to obtain journals, and rarely include detailed descriptions or adequate figures. Fortunately, many of these occurrences are listed in Dobruskina's (1994) review of the Triassic floras of Eurasia, and she indicates that several of these fos-

sils are probably not *Araucarites*. For example, several have been reassigned to *Tomioostrobus* Neuburg, 1936, which is a male lycopod cone. *Araucarites recubariensis* has been transferred to the extinct conifer genus *Voltzia* Brongniart, 1828, and *A. parsoraensis* has been transferred to *Samaropsis* Goeppert, 1864. The Triassic record of *Araucarites* from central and Western Europe is also ambiguous. Isolated bract/scales attributed to *Araucarites* have recently been figured by Kelber and Hansch (1995), but are poorly preserved and provide few points of comparison with the new Chinle species.

The Triassic *Araucarites* record from North America is poor. *Araucarites yorkensis* Wanner and Fontaine (1900), from the New Oxford Formation in Pennsylvania, is represented by one specimen showing only vague triangular impressions. The only other North American Triassic strobilar fossils assigned to the araucarians is *Primaraucaria wielandia* Bock, 1954, which is known from several articulated cones from the Triassic Richmond Basin



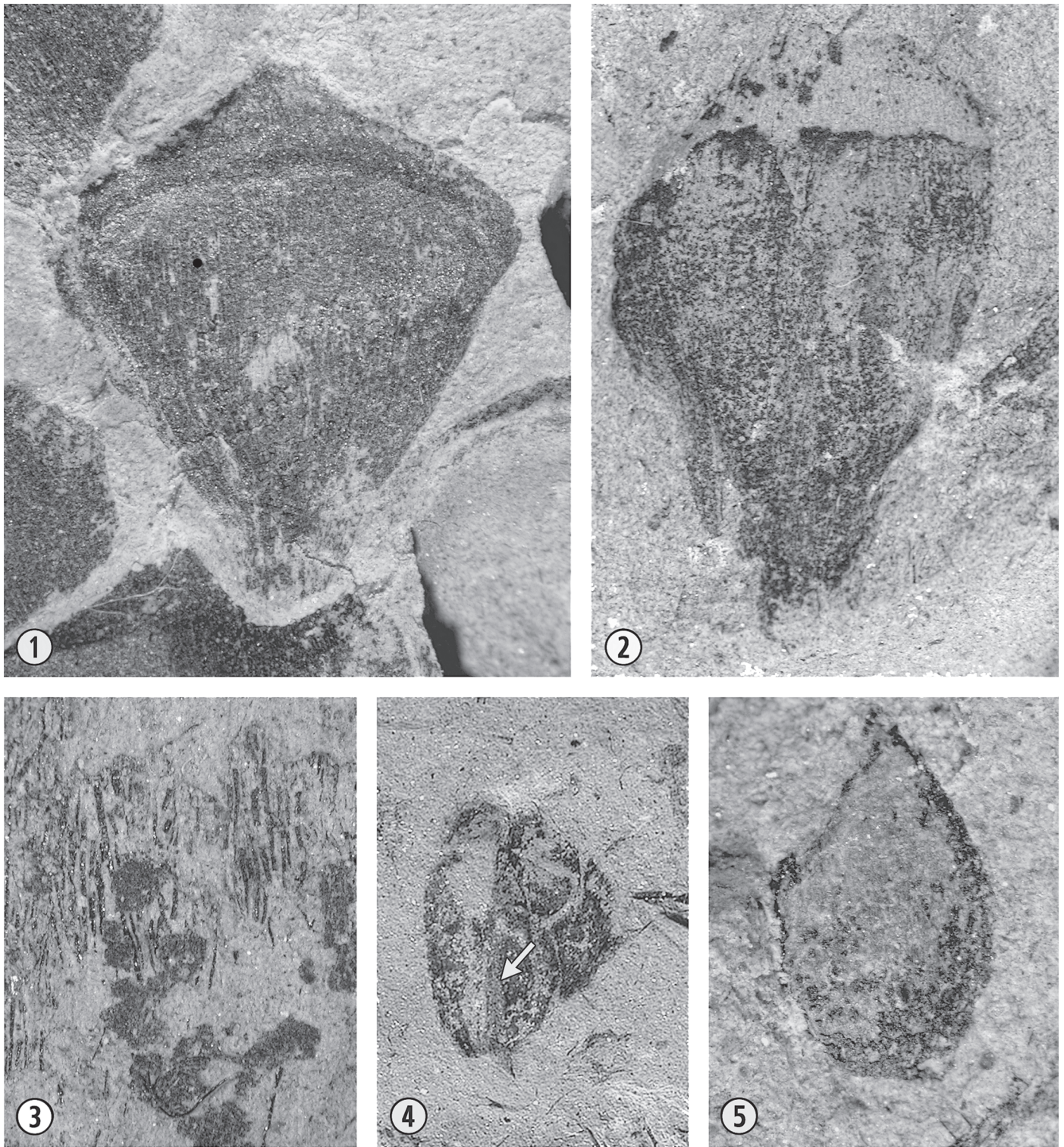


Figure 3. *Araucarites rudicula* sp. nov. 1. Detail of single bract/scale from holotype (Fig. 2.1) in abaxial view. The parallel vascular strands and/or fibers are clearly visible in this fossil. Note the well-defined transverse furrow and nearly complete mucronate apex.  $\times 8$ , PEFO 34141A; 2. Isolated bract/scale with poorly preserved apical extension.  $\times 7$ , PEFO 34145; 3. Internal tissues of a bract/scale showing parallel vascular strands and/or fibers.  $\times 20$ , PEFO 34144; 4. Isolated bract/scale in slightly oblique adaxial view showing ovule attachment scar (arrow).  $\times 2$ , PEFO 34144; 5. Isolated seed associated with *A. rudicula*.  $\times 15$ , PEFO 34145.

of Virginia. Unfortunately, many of the specimens of *P. wielandia* are now lost (Spamer, 1995). However, Cornet (1986) briefly reconsidered this fossil, and although its true affinities remain uncertain, it is unlikely that *P. wielandia* is

a conifer.

The only description of a Triassic *Araucarites* that includes articulated cones of which we are aware of comes from the classic Scoresby Sound locality of east Greenland



(Harris, 1935). Material of *A. charcoti* Harris, 1935 consists of a single elongate cone 6.0 cm long and 2.5 cm wide, and many isolated bract/scales. Based on figures in Harris (1935, Fig. 44), the bract/scales show considerable variation in shape and size; however, they are all essentially diamond-shaped. Some of the smaller scales are in the size range of *A. rudicula*, but most are nearly twice as large. There is a convex transverse furrow across the broadest part of the bract/scale similar to that of *A. rudicula*, but this occurs close to the middle region instead of at the apex. The area distal to the ridge (the apical extension) is relatively weakly lignified like that of *A. rudicula*; however, in *A. charcoti*, the most distal portion tapers more gradually to an acute tip. Also, the base of the apical extension on *A. charcoti* forms two extensions on each side that point back toward the cone axis. Most of the *A. charcoti* bract/scales taper proximally to a narrow base; however, there is no distinct stalk-like base, as in *A. rudicula*.

*Araucarites rudicula* bears a distinct resemblance to cones known as *Compsostrobus neotericus* Delevoryas and Hope, 1973 from nearly coeval deposits of the Pekin Formation of North Carolina. Both cones are elongate with stalked lateral appendages, but *Compsostrobus* is less laxly organized. The lateral appendages of both cones are interpreted as fused bract/scales, and are similar in consisting of a spatulate proximal region and elongate distal portion (Delevoryas and Hope, 1987). However, the "shoulders" (i.e., the edges of the widest portion) of the *Compsostrobus* appendages are more rounded than in *A. rudicula*. The spatulate region of the *Compsostrobus* appendage is interpreted as a cone scale, and the elongate portion as the subtending bract. These structures are intimately fused, and were apparently shed from the cone as a unit. In *Araucarites* the spatulate region is formed by the curved transverse ridge on the lateral appendage, which is unlikely to represent an entire cone scale margin, as it is visible on the adaxial and abaxial sides of the appendage (i.e. it would be obscured on the adaxial side by the subtending bract if it were a cone scale margin). The adaxial surface of the *Compsostrobus* cone scale bears two inverted ovules with elongate micropyles. The ovules have left two distinct scars on the adaxial scale surface in contrast to a single ovule scar of *A. rudicula*. According to Delevoryas and Hope (1973; 1987), the unlobed cone scale of *Compsostrobus*, which bears two inverted ovules, suggested affinities with the Pinaceae. This determination is somewhat strengthened by the associated pollen cones known as *Millerostrobus pekinensis* Taylor et al., 1987, which bear two abaxial pollen sacs per microsporophyll, and bisaccate pollen. Although the similarity of *Compsostrobus* ovulate cones to *A. rudicula* is at first striking, the details of the lateral appendage structure and ovule attachment are dif-

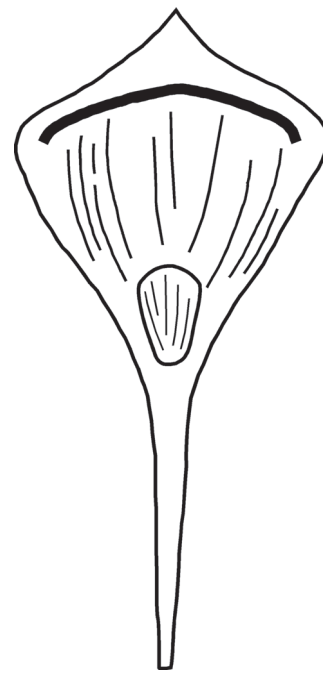


Figure 4. Reconstruction of an *Araucarites rudicula* sp. nov. bract/scale bearing a single small seed near the base of the distal portion. The transverse furrow is indicated by the broad line in the upper part of the drawing; some of the parallel vascular strands and fibers on the bract/scale and striations on the seed are indicated by narrow longitudinal lines.  $\times 4$ .

ferent and preclude a close phylogenetic relationship. Furthermore, pollen cones and shoots like those attributed to *Compsostrobus* have not been found to date in the Chinle Formation.

The Jurassic impression/compression record of araucarian conifers is much richer, and a few relevant species from this time are considered in relation to *A. rudicula*. A relatively large number of anatomically preserved araucarian cones from the Jurassic have also been described, but most of these are essentially similar to extant araucarians. Furthermore, the descriptions focus mainly on the anatomical details rather than gross morphology, which makes comparisons with the Triassic fossils impractical. The bract/scales of *A. rudicula* are rather similar, except in size, to those recently attributed to *Araucarites* n. sp. from the Early Jurassic of southeastern Utah (Tidwell and Ash, in press). Although the Utah specimens are generally slightly larger (8-12 mm wide, 11-12 mm long), they have nearly the same morphology; however, each bract/scale bears a much larger (5-6 mm wide, 8 mm long) obovate seed that occupies the lower two thirds of the structure. In addition, the Utah bract/scales lack a distinct basal stalk.

Nearly all of the cones from the Jurassic known from articulated specimens tend to be compact and ovoid, and thus more like those of extant araucarians. Therefore, points of comparison with *A. rudicula* must be based mainly upon the bract/scale morphology. The only species of which

we are aware with any particular points of comparison to *A. rudicula* are the similar species *A. phillipsi* Carruthers, 1869 and *A. brodiei* Carruthers, 1869, both of which come from the Middle Jurassic of England. *Araucarites phillipsi* was originally described from the classic Jurassic deposits of Yorkshire. Subsequent studies by Kendall (1949) and Harris (1979) provide more detailed information, including descriptions of the cuticles. The most striking similarity between *A. phillipsi* and *A. rudicula* entails the apical region of the bract/scales, which in both species is strongly truncated to form a short, apical point (i.e. mucronate). Therefore, the widest portion of the fossils in both species occurs close to the apex. The drawings in Kendall (1952) and Harris (1979) also show longitudinal striations that may indicate parallel vascular strands and/or fibers like those of *A. rudicula*. The *A. phillipsi* bract scales are also in the same size range as *A. rudicula*. However, the *A. phillipsi* specimens have a wing-like marginal membrane like that of many other Jurassic-Recent araucarians, and there is no distinct, stalk-like basal portion like that of *A. rudicula*.

*Araucarites brodiei* was originally from Stonesfield, Oxfordshire and has recently been reconsidered by Cleal and Rees (2003). The bract/scales of this species are similar in shape to those of *A. rudicula*, having the broadest part near the apex. The apex of *A. brodiei* is also weakly lignified and mucronate, and the ovule is oblong and positioned near the base of the bract/scale. However, the bract/scales of *A. brodiei* are more than twice as large as those of *A. rudicula*, and no distinct, stalk-like base is present.

Although there are many additional *Araucarites* species mentioned in the literature (e. g., Srivastava et al., 2004), those considered here are the only ones of which we are aware that exhibit any particular points of similarity to *A. rudicula*. We submit that the most distinctive feature of *A. rudicula* relative to other conifers with probable araucarian affinities is the distinct stalk-like basal portion of the bract/scales. However, these stalks are apparent only on articulated specimens and appear to be broken off or otherwise not preserved on the isolated bract/scales. Considering that most Triassic records of *Araucarites* are of isolated bract/scales, it cannot be definitively stated that such basal stalks are unique to *A. rudicula*. In fact, Kelber and Hansch (1995, Fig. 249) figured a supposedly aberrant bract/scale from the German Keuper with an elongated basal stalk as in our specimens. Perhaps the presence of basal stalks is a primitive feature lost in all post-Triassic forms.

More detailed comparisons with additional *Araucarites* species will not be practical until specimens of *A. rudicula* with preserved cuticles and attached seeds are found. Clearly, an exhaustive review of the entire genus *Araucarites* based on re-examinations of the actual fossils is also needed, especially the putative Paleozoic and Trias-

sic records, but this is beyond the scope of the present study. Therefore, comparisons with *A. rudicula* must be based for now on the few impression/compression fossils from the Triassic and Jurassic for which reliable, accessible descriptions are available as noted above.

#### Family Uncertain CREBERANTHUS gen. nov.

*Type species.*—*Creberanthus bealeii* sp. nov. by monotypy

*Diagnosis.*—Cone consisting of a narrow straight axis bearing loosely arranged synangiate organs. Synangiate organs composed of narrow proximal stalk and a distal rectangular synangia containing a single row of several narrow elongate pollen sacs. Pollen sacs containing large, bisaccate grains.

*Etymology.*—The genus is named in honor of Geoffrey Creber for his contributions to our understanding of the Chinle flora and for collecting some of the material described here. The root “*anthus*” refers to the microsporangiate nature of the cone.

*Occurrence.*—Blue Mesa Member of the Chinle Formation in Petrified Forest National Park.

#### CREBERANTHUS BEALEII new species

Figures 5-6

*Diagnosis.*—Cone at least 32.0 mm long and 12.0 mm wide, central axis 1.52 - 2.5 mm wide bearing loosely arranged synangiate organs branching in several planes; individual lateral organs consisting of a narrow, proximal stalk at least 2.2 mm long, and distal synangiate region, synangiate region elongate (typically about 1.5 times higher than long) ranging from ~ 2.5 mm high and 2.0 mm long to 3.0 mm high and 2.5 mm long, with biconvex to nearly straight lateral margins and straight proximal and distal margins, consisting of one row of 7-9 narrow, elongate pollen sacs with well-fused lateral margins; pollen bisaccate, typically 110 µm in diameter, ovoid, sacchi large with fine endoreticulations, broadly attached to corpus, distal colpus present.

*Etymology.*—The species *bealeii* is proposed in honor of Lt. E. F. Beale of the U.S. Army, who explored the region now including Petrified Forest National Park, and unsuccessfully tried to introduce camels as a mode of transportation in the West just before the American Civil War.

*Types.*—Specimen PEFO 34151, which represents an articulated cone (Figs. 5.1, 5.2, 5.5, 5.6) is here designated as the holotype. *In situ* pollen masses from this specimen (Figs. 6.1, 6.2., 6.4) are mounted on slide PEFO 34151a. A single grain (Fig. 6.3) is mounted on slide PEFO 34151b.



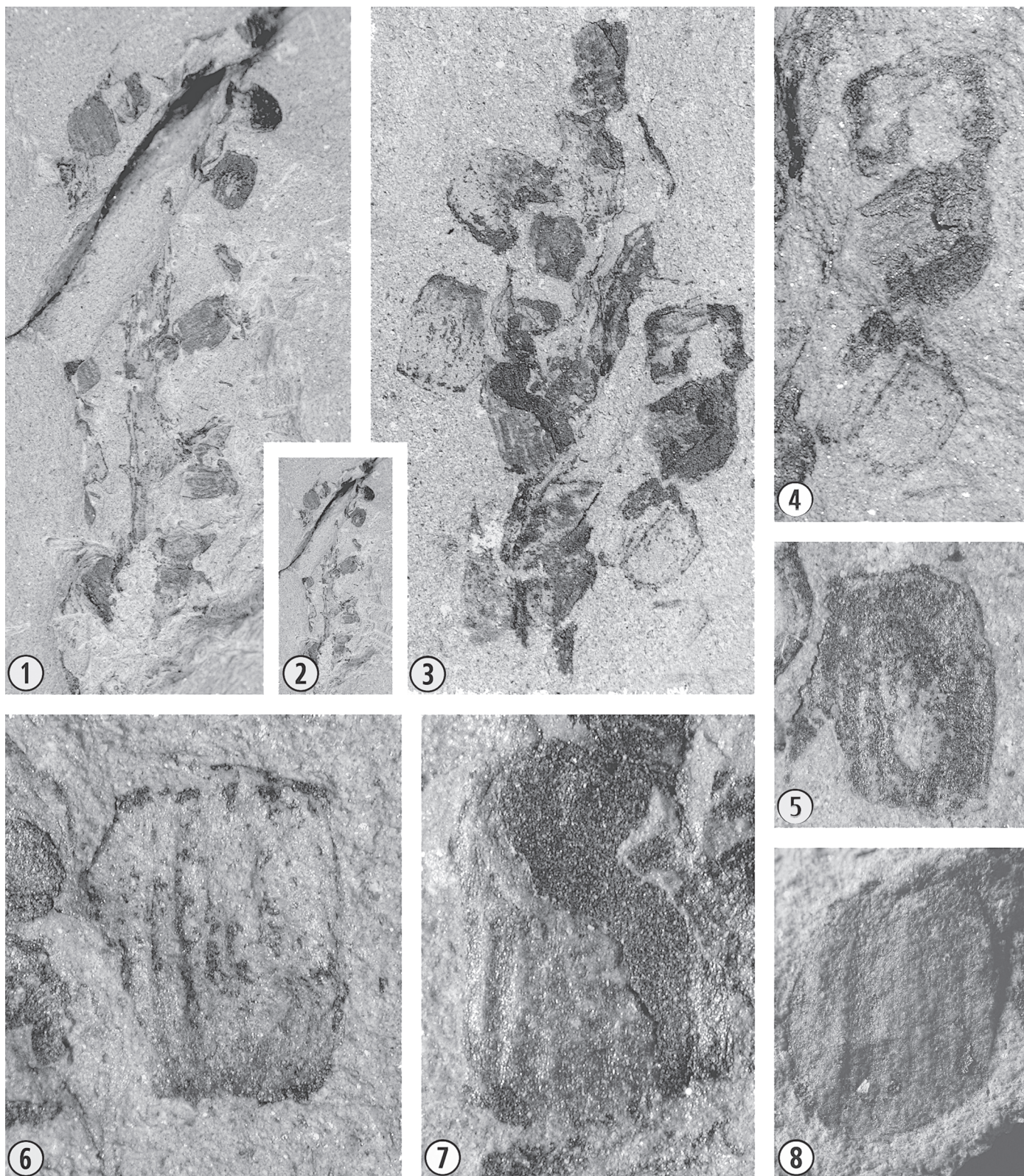


Figure 5. *Creberanthus bealeii* sp. nov. pollen organs from the Chinle Formation (Upper Triassic) of Arizona. 1. Holotype showing central axis and lateral synangia (arrow).  $\times 3$ , PEFO 34151; 2. Holotype at actual size. PEFO 34151,  $\times 1$ ; 3. Paratype with synangia oriented in a possible spiral arrangement.  $\times 6$ , PEFO 34152; 4. The synangia under extreme low angle light showing their preservation at different levels in the matrix.  $\times 8$ , PEFO 34152; 5. Detail of synangia from upper right of holotype (Fig. 5.1) showing relatively straight lateral margins.  $\times 13$ , PEFO 34151; 6. Detail of synangia with little organic material remaining except between several sporangial units.  $\times 18$ , PEFO 34151; 7. Detail of synangia showing striations on sporangia.  $\times 21$ , PEFO 34151; 8. Detail of synangium from holotype. Note strongly biconvex margins.  $\times 15$ , PEFO 34151.



Specimen PEFO 34152 (Figs. 5.3, 5.4) is the only additional cone known, and is designated here as a paratype. Pollen masses isolated from this specimen (Fig. 6.4) are mounted on slide PEFO 34152b.

*Occurrence.*—*Creberanthus bealeii* is presently known from two sites in the Blue Mesa Member of the Chinle Formation in Petrified Forest National Park. Specimen PEFO 34151 comes from locality PFP 004 of this paper and specimen PEFO 34152 comes from locality PFP 001.

*Description.*—Currently *C. bealeii* is represented by only two lax, articulated cones. It is not clear if the specimens are complete or only parts of larger structures. The holotype (Fig. 5.1) is ~32.0 mm long and 12 mm wide, with at least sixteen lateral synangiate organs. The second cone (Fig. 5.3) is ~17.0 mm long and 9.0 mm wide, with at least eleven lateral organs. Both cones possess an elongate central axis ~1.52–2.5 mm wide. Patches of black organic residue adhere to the axis, but no cuticles could be obtained by maceration of this material.

The arrangement of the lateral synangiate organs on the central axis is uncertain, as the stalks are not consistently preserved. On the holotype (Fig. 5.1), three lateral stalk bases are visible lined up on the left side of the axis, which could indicate a pinnate arrangement. However, the synangiate organs seem to occur at different levels of the matrix. Although there is no question that the distal synangia themselves occur at different levels on the paratype (Fig. 5.3), it is difficult to discern on most photographs because the matrix surface appears flat. Therefore, a view of the three synangia from the right side of the cone is shown under extreme incident light (Fig. 5.4), which clearly indicates that the basal synangium in the figure occurs at a lower level in the matrix. Furthermore, the variable orientation of the long axes of the synangiate portion of the lateral organs relative to the central axis on both cones is more consistent with a helical arrangement, but this is uncertain and will only be settled definitively by the discovery of more complete specimens.

The individual lateral organs consisting of a narrow, proximal stalk at least 2.25 mm long and 0.25 mm wide (based on longest preserved section from the holotype), and a distal synangiate region. The stalk expands slightly at the point of attachment to the synangiate region (Fig. 5.5). The synangiate region is recurved relative to the stalk and appears to be directly attached to the stalk apex with no indication of a lamina or any other sterile structure. The individual synangiate regions are elongate (typically about 1.3–1.5 times higher than long) ranging from ~2.5 mm high and 2.0 mm long to 3.0 mm high and 2.5 mm long, with biconvex (Figs. 5.8) to nearly parallel lateral margins (Fig. 5.7) and straight proximal and distal margins (Fig. 5.5, 5.6). Each synangiate region appears to consist of a single row of 7–9

narrow, elongate pollen sacs with well-fused lateral margins. The individual sporangia are most visible on the impressions under incident lighting and collectively create a pleated appearance (Fig. 5.5–5.8), which is somewhat obscured on specimens with abundant organic material adhering (Fig. 5.7). Fine longitudinal striations are visible on the impressions of individual sporangia (Fig. 5.7). The dehiscence mode of the individual sporangia could not be determined.

Several masses of *in situ* pollen grains were macerated from the organic matter covering the synangia from both cones. The most intact pollen mass recovered is elongate (at least 1.5 mm long and 0.44 mm wide) and composed of hundreds of tightly packed pollen grains (Fig. 6.1, 6.2), but it is broken off at the base. No overlapping pollen sacs have been found, which supports the interpretation of the synangium as having only a single row of sporangia. The individual pollen grains are large (average 139  $\mu\text{m}$  in diameter based on 20 randomly chosen grains in polar view) with a subcircular to ovoid amb due to the presence of two large, broadly attached sacchi with fine endoreticulations (Fig. 6.3). A distinct colpus is sometimes visible on the distal polar surface of the corpus (Fig. 6.2, 6.4, 6.5). The colpus is not always present on isolated grains (Fig. 6.3), but this is probably due to slight over-maceration. These pollen grains are most similar to the dispersed morphospecies *Alisporites opii* Daugherty, 1941; however, the average size of the *in situ* grains is larger (average 100–110  $\mu\text{m}$  vs. 130  $\mu\text{m}$ , respectively). This may not be significant, because Daugherty (1941) did not state how many grains he measured, and several of the *C. bealeii* grains are in the same size range.

*Comparisons.*—The general morphology of *C. bealeii* invites comparisons with the pollen organs of many so-called “pteridosperms,” which are generally thought to represent a paraphyletic and/or polyphyletic assemblage of Paleozoic and Mesozoic seed plants. Nevertheless, we submit that the general morphology of many “pteridosperm” pollen organs is more similar than generally conceded, and should be more seriously considered as a possible synapomorphy in future phylogenetic investigations. *Creberanthus bealeii* is particularly similar to species of the pteridosperm-like pollen organ *Pramelreuthia*, which occurs in the Chinle Formation, and we focus our comparisons on this genus. In fact, the similarity is great enough that we seriously considered describing *C. bealeii* as a new species of *Pramelreuthia*. Our justifications for not doing so are detailed below; however, these plants, and most other Mesozoic pteridosperms, remain poorly enough understood that any determinations should be considered tentative. *Pramelreuthia* is a distinctly pinnately organized pollen organ known from three Late Triassic species. The type species, *P. haberfelneri*, is based on a single specimen from

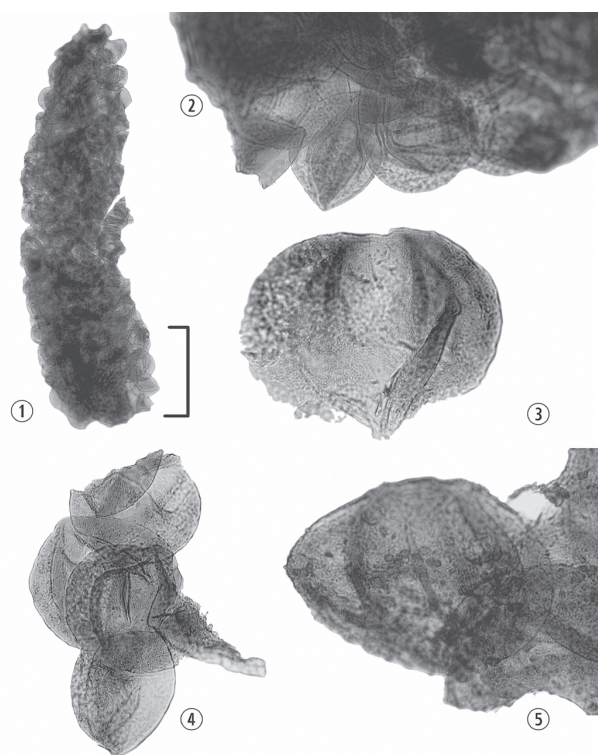


Figure 6. *In situ* pollen of *Creberanthus bealeii* sp. nov. from the Chinle Formation (Upper Triassic) of Arizona. 1. An *in situ* pollen mass, broken at the bottom. Bracketed area detail appears in next figure.  $\times 37$ , slide PEFO 34151a; 2. Detail of pollen grains from the bracketed edge of the pollen mass in Figure 6.1.  $\times 100$ , slide PEFO 34151a; 3. A single pollen grain in proximal polar view teased out from an *in situ* pollen mass.  $\times 250$ , slide PEFO 34151b; 4. An *in situ* pollen mass. Middle grain in distal polar view showing colpus.  $\times 150$ , slide PEFO 34152a.; 5. Detail of pollen grain with obvious colpus.  $\times 250$ , slide PEFO 34151c.

the classic Luntzerschichten deposits of Austria (Krasser, 1918; Kräusel, 1949). Two additional species, *P. dubielii* Ash and Litwin (1996) and *P. yazzi* Ash and Litwin (1996), are known from abundant material from five widespread localities in the Chinle Formation. One specimen of the small variety of *Pramelreuthia*, *P. yazzi*, occurs at locality PFP 004 of this paper in association with PEFO 34151.

The most obvious similarity between *Creberanthus* and *Pramelreuthia* is the presence of synangiate organs composed of laterally fused sporangia. This feature stands in stark contrast to the free condition of the sporangia in all other Mesozoic pteridosperm organs of which we are aware, including those of the Caytoniales, Corystospermales, and Peltaspermales. The synangiate condition is somewhat like that of several Paleozoic pteridosperms with probable affinities with the Lyginopteridales (e.g. *Crossothea* Zeiller, 1883) and Medullosales (e.g. *Whittleseya* Newberry, 1853) (Taylor, 1988). However, the non-striate bisaccate pollen of *Creberanthus* and *Pramelreuthia* clearly links these organs with other Mesozoic pteridosperm pollen organ taxa.

Well-fused synangia born on narrow stalks are

unique among Mesozoic pteridosperms and indicate a close relationship between *Creberanthus* and *Pramelreuthia*. However, we interpret the differences between the two types of fossils to be great enough to justify erecting the new genus *Creberanthus*. The most obvious difference is the shape of the synangiate organs. In *Pramelreuthia*, the synangiate organ is typically about 1.5 times longer than high, whereas those of *Creberanthus* are typically about 1.5 times higher than long. Furthermore, based on the limited material of *Creberanthus*, the synangiate organ appears to consist of a single row of synangia, whereas those of *Pramelreuthia* are certainly bivalved (Ash and Litwin, 1996). The pollen grains of *Creberanthus* are also distinctive in being much larger (average 110  $\mu\text{m}$ ) than those of any *Pramelreuthia* species. Finally, the suggested non-pinnate arrangement of the *Creberanthus* synangiate organs may represent a significant difference from the clearly pinnate structure of *Pramelreuthia*.

The only other Mesozoic pollen organ similar to *C. bealeii* is an unnamed species represented by anatomically preserved material in calcareous nodules from the Chinle Formation (Pigg et al., 1993). Although not well known, this pollen organ is synangiate and produces *Alisporites*-like pollen grains like *C. bealeii*. However, the synangia were probably composed of 10–12 pollen sacs, and the grains measure only 80  $\mu\text{m}$  in diameter. Nevertheless, it remains a possibility that this material represents the same plant as *C. bealeii* in a different preservational mode. More material of both kinds will be needed to resolve this question.

## CONCLUSIONS

Although fossils of *A. rudicula* and *C. bealeii* are rare, they may have implications for our understanding of the more common components of the Chinle flora. For example, *A. rudicula* provides the first convincing impression/compression evidence for araucarian conifers in the Chinle Formation. In addition to providing new data on Triassic araucarian morphology and biogeography, this discovery has obvious implications for the possible affinities of the famous *Araucarioxylon arizonicum* logs of Petrified Forest National Park.

Based on the *Araucarioxylon*-type wood anatomy, it has historically been assumed that the *A. arizonicum* logs of Petrified Forest National Park were produced by giant araucarian trees. This belief was reflected in reconstructions depicting the living trees with long, unbranched main trunks, and compact apical crowns like those of most modern *Araucaria* species. Remarkably, until recently, this concept was never tested by detailed observations of the numerous available logs. It was pointed out by Ash (1987) that the limbs of *A. arizonicum* did not occur in whorls as in

typical araucarian trees. Ash and Creber (2000) measured and examined many of the larger logs in Petrified Forest National Park, and found that substantial branch scars, and in some cases actual branch bases, occurred almost to ground level. Such a branching pattern, along with the clearly documented presence of a massive taproot, suggests an architecture at variance with that of other fossil and modern araucarians (Ash and Creber, 2000: fig. 3).

The new reconstruction of the *A. arizonicum* tree, along with the absence of definitive araucarian impression/compression remains in the Chinle Formation, appeared to cast doubt on the araucarian affinities of the parent plants. The wood anatomy remained suggestive, but *Araucarioxylon/Dadoxylon*-type wood is known even from non-conifers, such as the glossopterids. The discovery of the *A. rudicula* ovulate cones described here, however, suggests that araucarian conifers were part of the Chinle flora, although it cannot be proven at this time that they are definitively related to the logs. In fact, the rarity of the cones compared to the abundance of logs could be interpreted as evidence against such a relationship. In any event, the possibility that the logs are of araucarian affinity does not cast doubt on the Ash and Creber (2000) reconstruction of the trees, as it is based on observations of the fossil logs rather than assumptions of taxonomic affinity.

Coniferous foliage is rare in the Petrified Forest (Ash, 1989) and includes only *Brachyphyllum hegewaldia* Ash, 1973 and *Podozamites arizonicus* Daugherty, 1941. Of the two, *B. hegewaldia* is the only fossil which might be related to the Araucariaceae because Kendall (1949) clearly demonstrated that some of the Jurassic species of *Brachyphyllum* in England appeared to be araucarian (Har-

ris, 1979). However, it should be pointed out that *B. hegewaldia* is not very common in the Petrified Forest and is known from a single locality several km from the locality that contained *A. rudicula*. Thus, there is no strong evidence that the two fossils are in any way related.

The *C. bealeii* pollen organs are, like the conifer cones, extremely rare components of the Chinle impression/compression flora. However, the *in situ* pollen is essentially identical to *Alisporites opii*, which Daugherty (1941, p.98) claimed is the most common dispersed palynomorph in the Chinle Formation. Assuming *C. bealeii* was the sole source of this pollen, the parent plant must have been a more important component of the flora than indicated by the macrofossil record. This fossil, along with the two species of *Pramelreuthia* (Ash and Litwin, 1996) and the unnamed permineralized synangium (Pigg et al., 1993), reveal that pteridosperms were a more diverse and significant component of the Chinle flora than previously believed.

## ACKNOWLEDGMENTS

We are grateful to Dr. G. Creber for helping collect some of the material described here. The assistance of the superintendents of Petrified Forest National Park who authorized us to collect in the park, and the encouragement and assistance provided by members of the staff, is acknowledged with thanks. Petrified Forest Museum Association provided financial assistance with fieldwork. Aspects of this material are based on work supported by the National Science Foundation under grant EAR-0105476 to B. Axsmith. Sonja Axsmith provided invaluable assistance with the figures.

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